

Zwischen cricetinem und murinem Molarenmuster nimmt *Megadendromus* eine neue und wichtige Position ein. Danach scheinen Dendromurinae und Murinae bedeutend näher verwandt, als bisher anzunehmen war.

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## Combs, fur and coat care related to habitat in the Ctenodactylidae (Rodentia)

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#### Abstract

Described are the coat and toe combs of five species of gundi (Ctenodactylidae).

The length of the fur of the five species is negatively correlated with the mean minimum annual temperature of their habitat. It is suggested that in the northern Sahara the fur is important in insulating against the winter cold. The density of the fur protects against desert winds.

The structure of the individual hairs (cuticle, medulla and cross-section) is described. The structure differentiates the hairs from those of other mammals.

The characteristic combs on the two inner toes of the hind feet of the five species are described. Their use in coat care is discussed.

Gundis have sharp curved claws essential for gripping rocks but unsuitable for scratching soft fur. The toe combs take the place of claws in normal scratching activities.

## Introduction

GRAY (1830) first named the North African gundi-mouse *Ctenodactylus*, or comb-toe, on account of the 'tufts of rigid hair' on the inner two toes of the hind feet. For the same reason, BLYTH (1855) called the Ethiopian genus *Pectinator*. In describing the other two genera of the family, *Massoutiera* from Algeria and *Felovia* from Mali, LATASTE (1881, 1885) and ROSEVEAR (1969) doubted the presence of combs on the toes. But, in 1893, when ZITTEL invented the family Ctenodactylidae for the four genera, it was generally assumed that combs on the toes of the hind feet were characteristic of the family. Few other rodents have such tufts of bristles on their hind feet but they are found in the South American Chinchillidae and Ctenomyidae and in the South African Petromuridae.

The function of the comb is said to be for grooming and 'dressing the pelage' (PACKARD, 1967) and has been likened to a teasel brush (ROTH, 1956) but no exact descriptions of the combs of the different genera have been given nor of their use.

From observations of five species of Ctenodactylidae over the last ten years the problem can now be resolved.

In the course of these observations, a study was made of the fur to determine its properties and the need for coat care. The structure of the hairs proved a useful method of identification of remains of gundis in the faeces of predators.

## Material and methods

Five species of Ctenodactylidae, representing the four living genera, were used in this study. They were observed in their desert habitats and some of each species were kept in captivity at various times between 1967 and 1977 (GEORGE, 1974).

Observations and measurements in captivity were made on 26 *Ctenodactylus vali* (from Algeria), twelve of which were born and reared in captivity; four wild born *C. gundi* (from Tunisia), two adults and two juveniles; eight *Pectinator spekei* (from Ethiopia), two of which were observed from the age of one week to five years; twelve adult *Massoutiera mzabi* (from Algeria) and two juveniles reared from birth; twelve adult *Felovia vae* (from Mali).

There are three microscopic characteristics of hairs that, combined, can often identify the mammal from which they came. These are the cuticle scale pattern, the medulla pattern and the shape of the cross section of the hairs. Tip, shield and base of the hairs tend to be uniformly patterned throughout the rodents (DAY, 1966) but the upper shaft bears the characteristic pattern of the animal.

Hairs were taken from the back and cleaned in 70% methanol. Clean hairs mounted directly on a slide show the medulla pattern. Hair width was measured on these preparations.

Cuticular pattern was studied by making a cast of the hairs in 5% gelatine. Cuticle patterns have been described and classified by HAUSMAN (1920, 1924), WILDMAN (1954), DAY (1966) and BRUNNER and COMAN (1974) and consequently the same pattern has been given several names. The nomenclature of BRUNNER and COMAN is followed here.

Sections of hairs were made according to the method described by WILDMAN (1954). A small bundle of hairs was embedded in necoloidine solution and sectioned in a Hardy microtome made by the Wool Industries Laboratories. Mounted in 70% methanol, the general outline of the hair section can be seen at a magnification  $\times 10$ .

The length of the coat pile was measured with a fine calibrated rod on living animals in which the hair had been gently blown into an upright position. The majority of the hairs,

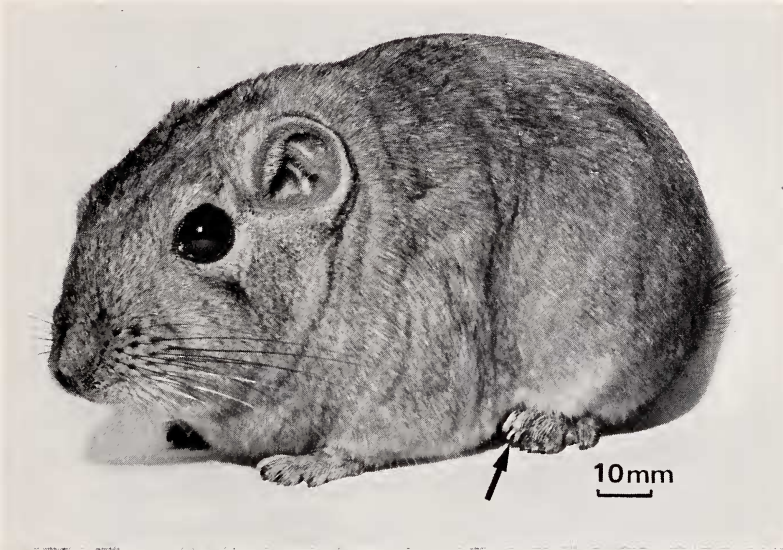


Fig. 1. *Ctenodactylus vali* showing the combs on the two inner hind toes. The arrow points to the lower combs on the two toes. The upper combs are just visible under the rows of long bristles

like those of many other small rodents, are sharply kinked several times along their length. The measured length of the coat pile is not, therefore, the length of the individual hairs. For each animal, measurements were made of the fur on the back, the flank and the thigh. Five measurements were made and the average used in the final analysis.

Fur density was estimated by pulling a tuft from a near middorsal point lateral to the vertebrae and anterior to the ilium. An area about  $2 \times 2$  mm was cleared of fur and the bare patch measured with calipers. The patch was photographed and measured again. The hairs of the pulled tuft were counted. Five samples were taken from each species.

Pieces of skin from the back, flank and foot pad were fixed in Bouin's fluid, sectioned at  $10 \mu\text{m}$  and stained with haematoxylin and eosin.

Ctenodactylids have four digits on both fore and hind feet. The combs are conspicuous on the two inner toes, digits 2 and 3, of the hind feet (Fig. 1). The combs and rows of bristles that cover the combs were removed for closer examination.

Direct observations were made of the use of the combs in the wild and in captivity: 8 mm colour film was taken of all five species and was analysed for comb use.

Meteorological data was obtained from the nearest airstrip, plantation or research station and, where appropriate, supplemented from Meteorological Office published data (1967).

## Results

### Hair structure

Ctenodactylid hair scales have smooth margins, the margins are distant from one another. The pattern conforms to the narrow petal (Fig. 2b).

The medulla is of the commonest rodent type: the rodent base of MATHIAK (1938), the compound medulla of MEYER (1952), the multiseriate of DAY (1966) and the wide aeriform lattice of BRUNNER and COMAN (1974). In this type of medulla, the cells have shrunk and left big air spaces (Fig. 2a).

In cross section, ctenodactylid hairs are oblong to oval and the medulla is seen to be divided (Fig. 2c). There is no appreciable difference between the species. The combination of hair characteristics provided a good method of identification.

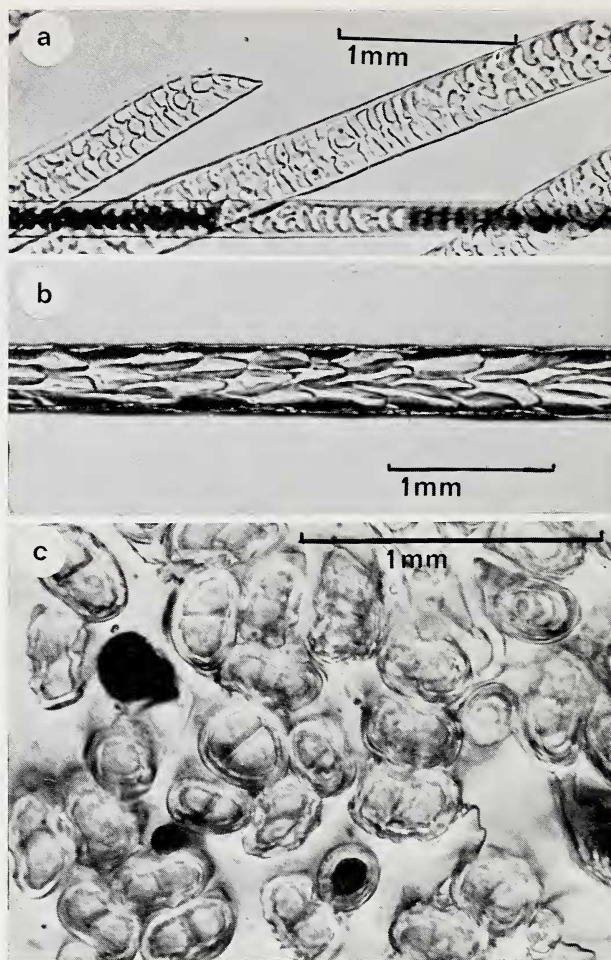


Fig. 2. Hair structure: a = wide aeriform medulla lattice, *Ctenodactylus gundi*; b = petal scales, *Pectinator spekei*; c = oblong-oval transverse section of hairs, *Ctenodactylus vali*

### Fur length

The length of the back and flank fur proved to give the most uniform results. The length of the pile varies in the five species and shows a correlation ( $r = 0.995$ ,  $P < 0.001$ ) with the mean annual temperature of the animal's habitat (Table 1).

There was no significant difference in the length of fur of animals caught in March and July in the Sahara nor was there any significant difference in the length of fur after five years in captivity.

Young *Ctenodactylus vali* and *Massoutiera mzabi* have shorter fur than the adults but it is relatively longer if it is compared with the overall length and weight of the animal. Juvenile fur, during the first month of life, is 70–80 % of the length of adult fur at a time when the body weight reaches only 15–20 % of the adult.

The average width of each hair is correlated with fur length (Table 1).

Table 1  
Fur characteristics and climate of the habitat

	adult mean weight (g) ± s. e.	mean maximum temp. (°C)	mean minimum temp. (°C)	mean adult hair length (mm) ± s. e.	range of hair widths (mm)	mean angle of kink (°)	mean no. guard hairs per 1,000 hairs ± s. e.	mean density hairs/(cm <sup>2</sup> ) ± s. e.	mean wind speed (km/h)
<i>Ctenodactylus gundi</i>	288.8 ± 8.5 (n = 2)	26	12.2	17 ± 0.3	0.050—0.034	39	3.2 ± 0.4	23,220 ± 443	—
<i>Massoutiera mzabi</i>	182.6 ± 12 (n = 11)	27.9	14.4	16 ± 0.5	0.049—0.025	46	1.2 ± 0.2	26,965 ± 235	13
<i>Ctenodactylus wali</i>	172.8 ± 6.6 (n = 14)	29.4	15.9	14 ± 0.5	0.043—0.020	45	2.5 ± 0.3	17,664 ± 352	10
<i>Felovia vae</i>	185.8 ± 8 (n = 10)	36.5	22.2	6.5 ± 0.5	0.038—0.019	57	2.5 ± 0.2	8,817 ± 316	6
<i>Pectinator spekei</i>	178.2 ± 0.9 (n = 4)	35	23.2	6 ± 0.6	0.034—0.021	33	1.7 ± 0.2	25,586 ± 639	10

### Fur density

The hairs in all five species are grouped and each group leaves the skin by a single depression as in jerboas (GHOBRIAL, 1970), chinchillas (WILCOX, 1950) and camels (LEE and SCHMIDT-NIELSEN, 1962). The number of hairs in a group varies from one to six (Fig. 3). *Pectinator* has more groups of four to six hairs than the other species (Table 2). When four or five hairs come out together in *Pectinator* one hair is often a very short one.

The average density of the fur for the five species is shown in Table 1. There is no correlation between density and mean annual temperature of the habitat but some relationship between wind speed and fur density.

### Comb structure

In the type species, *Ctenodactylus gundi*, the lower combs, immediately above the claws, are short and strong and made up of five bristles. On both digit 2 (first toe) and digit 3 (second toe) the bristles are on average 3 mm long. They are laterally compressed, more or less oblong in section, about 0.4 mm at the base and curved to form the 'teeth' of the comb. Above these combs, on each of the two inner digits, are the upper combs. The six bristles are longer and finer than on the lower combs but they are flattened and curved. Above the short strong combs there is a row of nine longer more slender bristles, similar in structure to the bristles on the other hind toes. Above these again is a row of nine, merging into other stiff bristles at the side of the toes.

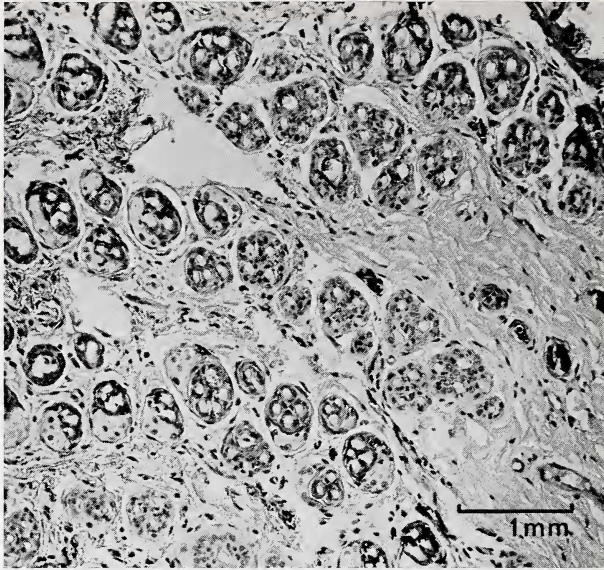


Fig. 3. Section through the skin of *Pectinator spekei* showing the arrangement of the hairs in bundles

Table 2

Number of hairs emerging in a group  
(sections made from one adult male and one adult female of each species)

		Number of groups counted				
		<i>Ctenodactylus gundi</i>	<i>Felovia vae</i>	<i>Massoutiera mzabi</i>	<i>Ctenodactylus vali</i>	<i>Pectinator spekei</i>
Number of hairs per group	1	35	24	55	72	50
	2	70	100	82	63	60
	3	100	100	66	39	50
	4	5	4	9	15	64
	5	0	0	1	12	18
	6	0	0	0	0	2

Finally, another row of nine merges into the fur of the leg. All the bristles are unpigmented (Fig. 4 and 5a).

*Ctenodactylus vali*, a much smaller animal, has grey combs with shorter thicker bristles (Fig. 5b). The upper rows are unpigmented (Fig. 1).

The combs and bristles of the other three genera are remarkably similar to those of *Ctenodactylus*. The upper combs of *Felovia* are less developed than those of the other species (Fig. 5d).

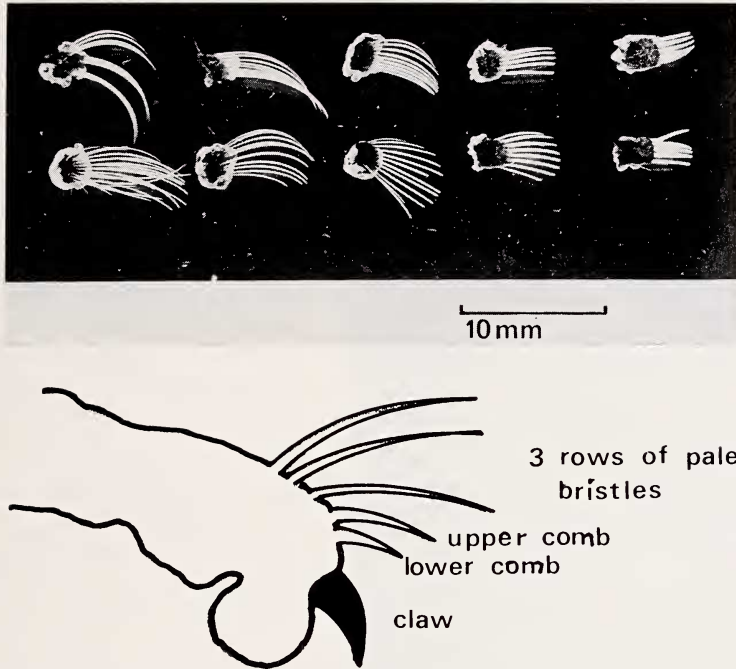


Fig. 4. Above: The combs and toe bristles of the right hind foot of *Ctenodactylus gundi* seen from above. From right to left: lower combs of the two inner digits, upper combs, three rows of long pale bristles. Below: Side view of the arrangement on the toe

The upper bristles show some individual variations in both colour and number though there are always between nine and twelve in each row. The majority are unpigmented which makes them a conspicuous feature on the dark toes of *C. vali*, *Pectinator* and *Felovia*.

The only significant difference is found in *Pectinator*. In this species there is an extra row of six short (2.5 mm) stiff bristles below the lower comb on each of the comb digits (Fig. 5e). Thus, *Pectinator* is the only member of the family to have three-tiered combs, a feature described by PETERS (1871) but attributed to *Ctenodactylus* by several authors (POCOCK, 1922; GRASSE and DEKEYSER, 1955; ROTH, 1956).

#### Comb use

All ctenodactylids scratch with their hind feet. Scratches can be classified as head, flank, belly and rump scratches.

An average scratch lasts  $2.25s \pm 0.3$ . Scratches may be fast or slow: on average, either 20 strokes a second or about 11 strokes a second which is comparable to the fast and slow scratches made by mice.

In scratches of the head and flank, the hind leg is brought forward and the head or flank turned towards the leg while the animal stands on three legs. The sharp claws are turned under and the combs of the inner toes come in contact with the fur. For belly and under-arm scratching the animal sits back and is supported on two legs during a very rapid scratch with the combs.

The rump scratch is characteristic of the ctenodactylids. The animal stands on three legs with its weight forward and the free hind leg scratches the rump of the

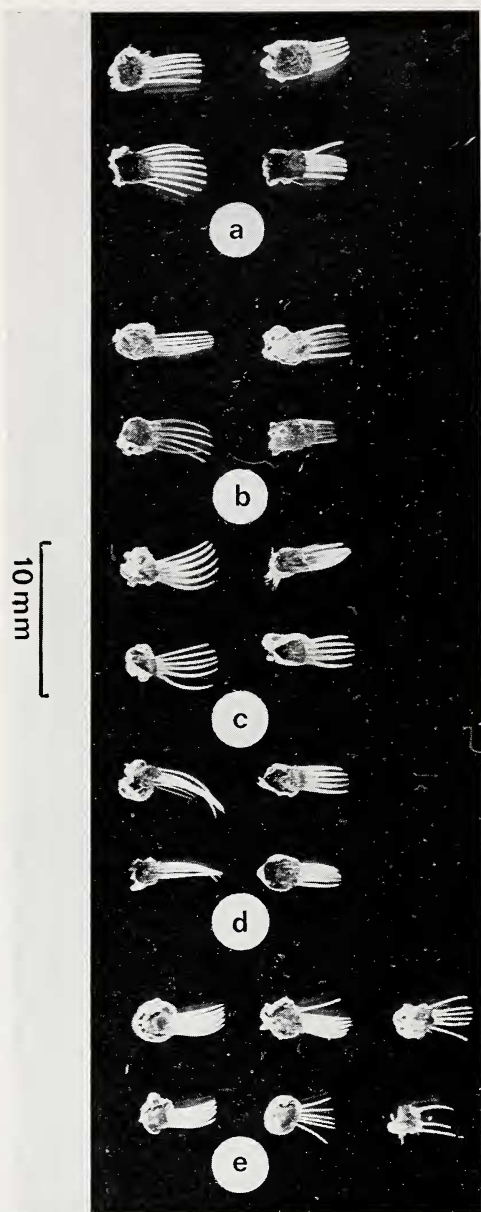


Fig. 5. The combs of the right hind foot of five species of ctenodactylid seen from above. Lower combs on the right, upper combs on the left. a = *Ctenodactylus gundi*; b = *C. vali*; c = *Massoutiera mzabi*; d = *Felovia vae*; e = *Pectinator spekei*

opposite side. The scratching leg extends backwards and towards the centre line which brings the top of the foot, with the combs, in contact with the fur (Fig. 6b and 6c). The scratch can be considered as a three stroke movement though it is, in practice, continuous. There is an up stroke of the leg, a down stroke and a retraction stroke. Sometimes the retraction stroke is omitted. In rapid scratching each stroke can occur about eight times a second and the whole movement gives the impression of a rapid circling scratch. At all times, the position of the foot brings only the combs in contact with the coat.

From observations of animals in the wild, the average number of rump scratches is about six an hour.

## Discussion

Long dense fur makes an ideal insulation for cold nights and hot windy days in the desert. The correlation between the length of the fur and the mean annual temperature of the habitat (Table 1) seems to support this.

According to SCHOLANDER (1955) the length of fur of a small mammal can rarely exceed 30% of the radius of the animal. Above that figure the fur gets in the way of movement and soon becomes too heavy. Rough calculations

of the radius of several living ctenodactylids were made. When the three northern species tuck in their extremities in the cold they approach a sphere in shape. *Pectinator* and *Felovia*, although of the same average weight as *C. vali* and *Massoutiera*, are longer lankier animals and the calculations of their radii are less realistic. Table 3 shows the calculated maximum length of fur for body radius and the actual length. The two figures are reasonably close for the three northern species. It can be presumed, therefore, that the northern ctenodactylids are carrying about the maximum fur length for their size.



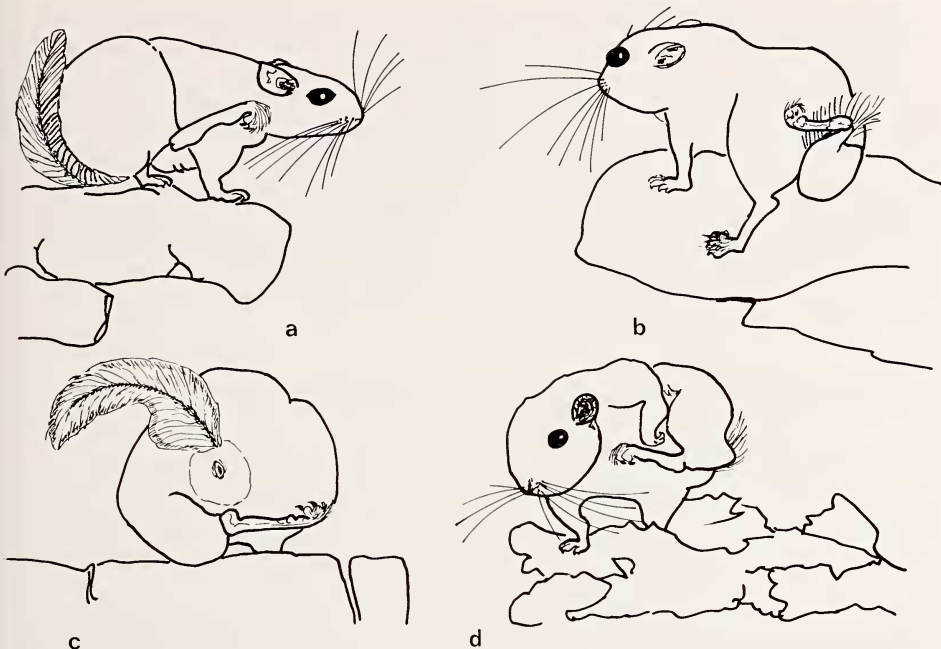


Fig. 6. Ctenodactylids scratching with their toe combs. Drawn from film strips. a = head scratch, *Pectinator spekei*; b = rump scratch, up-stroke, *Felovia vae*; c = rump scratch down-stroke, *Pectinator spekei*; d = under arm scratch, *Massoutiera mzabi*

For mammals weighing between 200 and 300 g the critical air temperature, below which the basal metabolism of the animal must increase to maintain body temperature, varies from about 23°C to 21°C according to the formula  $T_B - T_C = 4W^{0.25}$  (SCHOLANDER et al., 1950; BARTHOLOMEW, 1968). Ctenodactylids have a body temperature of 37.4°C and the critical temperature gradient would be about -14°C. Below the lower critical temperature, SCHOLANDER et al. (1950) found critical temperature gradients to range between -13°C and -20°C for mammals of gundi size. The lower gradient was typical of tropical mammals.

*Pectinator* and *Felovia* are unlikely to meet temperatures below 23° in the daytime on more than a few days a year whereas the three northern species may have to live through three winter months when the maximum daytime temperature is below 23°C. When the temperature is very low and there is no sunshine, gundis

Table 3

Fur length in relation to estimated radius of the animal

	radius of animal (mm)	estimated maximum fur length (mm) (0.3r)	measured fur length (mm)
<i>Ctenodactylus gundi</i>	50	15	17
<i>Massoutiera mzabi</i>	45	13.5	16
<i>Ctenodactylus vali</i>	43	12.9	14
<i>Felovia vae</i>	45	13.5	6.5
<i>Pectinator spekei</i>	42	12.6	6

may not emerge from their rock shelters for a day or two but, as they do not store food either in the form of fat in their bodies or in their shelters, they are forced out eventually to forage. However, in adverse conditions, they emerge only in the warmest part of the day. The lowest temperatures they are likely to encounter under these circumstances are  $11^{\circ}\text{C}$  and this must be exceptional. Assuming that they do have to meet midday temperatures near the mean minimum for the habitat, it is calculated that the length of fur provides almost exactly the right amount of insulation to maintain body temperature without increasing the basal metabolism (Table 4). Clearly, then, there will be very few occasions in the life of a ctenodactylid when the basal metabolism will not meet the temperature needs of the animal.

Table 4

Temperature gradients calculated for fur thickness and mean minimum temperature of the habitats in the North Sahara

Ctenodactylid body temperature ( $T_B$ ) is  $37.4^{\circ}\text{C}$

	lower critical body temperature $T_C$ $T_B - T_C =$ $4W^{0.25}$	fur length $f$ (mm)	mean minimum temperature $T_S$ ( $^{\circ}\text{C}$ )	winter gradients encountered $\frac{T_B - T_S}{f}$
<i>Ctenodactylus gundi</i>	20.9	17	12.2	-14.8
<i>Massoutiera mzabi</i>	22.5	16	14.4	-14.3
<i>Ctenodactylus vali</i>	22.9	14	15.9	-15.3

The oval to oblong cross section of the individual hairs, the kinked form of the majority of hairs and the complex medulla pattern also provides for good air retention and insulation. The petal pattern of the hair scales provides a strengthening for the very fine hairs, permitting high density long fur. Even *Felovia* fur is twice as dense as that of a European rabbit (TREGGAR, 1965).

TREGGAR showed that insulation in winds depends only on the density of the fur. The conductivity of very dense fur is unaffected by wind as the air between the hairs remains undisturbed except at the surface. The average wind speeds for the habitats are shown in Table 1 for four species. No data is available on wind speed for the Tunisian habitat of *Ctenodactylus gundi* but it is likely to be close to that of the *Massoutiera* habitat. Although the mean annual wind speed is not high for any of the localities, it is significantly lower for *Felovia* which may account for its significantly less dense fur. The other three species encounter periods of high winds which may last for three or four consecutive days in several months of the year. The wind rarely exceeds 17 km/h in the *Felovia* habitat.

Ctenodactylid fur seems to be less important as an insulation against excess heat. Gundis avoid rises in body temperature by their behaviour and by sweating. They are rarely active or exposed at temperatures above  $35^{\circ}\text{C}$ . The temperature of their rock shelters is usually well below this. The majority of ctenodactylids are sand-coloured but this is camouflage rather than for its heat reflective properties. Several colonies of *Pectinator* are dark grey and live among dark grey lava rocks.

During an inadvertent experiment with several captive colonies of *C. vali* and *M. mzabi*, the ambient temperature reached 42 °C for eight hours. The species with the shorter hair, *C. vali*, was the one that survived.

However, the long dense fur obviously provides protection against ultra-violet light penetration (LEE, 1972) and it may be significant that *Felovia* with a short, relatively sparse coat, is the only species with a pigmented body skin.

It is concluded that the fur provides a good insulating material for these diurnal desert rodents and length and density have been selected by the prevailing climatic conditions in the different habitats.

In order to provide this insulation, the fur must remain intact, dry, clean and unmatted. There is little protection from guard hairs (Table 1). The limited amount of rain they encounter would seem to obviate the need for guard hairs of the density of a European rabbit (5 %).

It might be expected that, as coat care is so obviously important to maintain insulation, the special combs on the hind toes would be used for "cleaning and arranging the long loose fur" (ROSEVEAR, 1969). But this is only partially true.

Gundis keep their fur in good condition in the same way as many rodents that have no combs on their toes. The fur must be kept dry but this is not a problem in a desert climate. The most important coat care activity is rolling in fine sand. Gundis kept warm and dry on sawdust or on coarse silver sand are not able to maintain their coats in good condition. The hairs become matted.

The head is cleaned by stroking with two front legs together and the long vibrissae and nose are cleaned by wiping with one front foot, sometimes passing the vibrissae between the digits.

Why, therefore, have toe combs?

The answer is a negative one. Gundi feet are armed with strong sharp claws that grip irregularities on the rocks as they climb. Gundi fur comes out easily and forms a useful defence for animals that have few projections to leave behind in the mouth of a predator. Like any other rodent, gundis scratch to remove parasites and other foreign bodies from the coat.

Scratching easily detached fur with sharp claws is impractical, causing bare patches and destroying the important insulating qualities of the coat. Normal scratching is, therefore, effected by the combs with the claws turned under. The use of the dorsal toe combs gives the characteristic gundi rump scratch and extends scratching to all areas of the body.

Ctenodactylid toe combs are for scratching without making bare patches. They are not for grooming or "brushing away sand when digging burrows" (BURTON, 1962). They do not dig burrows and they brush away sand with their front feet.

It is significant that the chinchillids, *Ctenomys* and *Petromus*, the only other rodents reported to have toe combs, have very soft fur. It may also be significant that all have at one time or another been classified as hystricomorph rodents.

### Zusammenfassung

#### *Zehenkämme, Fell und Fellpflege in Beziehung zum Lebensraum bei Ctenodactylidae (Rodentia)*

Beschrieben werden Fell und Zehenkämme von fünf Gundi-Arten (Ctenodactylidae).

Die Felldicke der Arten ist mit der mittleren Minimaltemperatur in ihrer Heimat eng negativ korreliert. Das legt die Annahme nahe, daß in der Sahara die Wärmeisolation durch das Fell im Winter eine wichtige Rolle spielt.

Die Struktur einzelner Haare (Cuticula, Mark, Querschnitte) wird beschrieben. Die Merkmale dürften die Unterscheidung von Haaren anderer Säugetiere ermöglichen.

Die für die Familie charakteristischen Zehenkämme aus Borsten an den beiden Innen-

zehen der Hinterfüße kommen in ähnlicher Ausprägung bei allen fünf Arten vor. Ihre Funktion bei der Fellpflege wird beschrieben. Offensichtlich sind die im Zusammenhang mit dem Felsklettern verlängerten, sehr spitzen Krallen hierzu ungeeignet und wurden daher durch die Borstenkämme in der Fellpflege ersetzt.

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## Beobachtungen zur Tagesperiodik von Wild- und Hauskaninchen

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### Abstract

#### *Observations on the 24-hours-rhythm of wild and domestic rabbits*

Studied the differences in circadian rhythm of activity and feeding between wild and domestic rabbits.

Six 24-hours-observations were carried out in 2 wild and 4 domestic rabbits kept in open-air fences.

During 24 hours wild rabbits show a periodical turn between one phase of total rest and another phase of nearly uninterrupted activity. Domestic rabbits, on the contrary, show a rapid change of short restings and active phases. During the hours of daylight domestic rabbits always show more or less activity, whereas, on the whole, wild rabbits are only active at night. Among representatives of the domesticated form there are remarkable individual differences in the rate of nocturnal to diurnal activity. Wild rabbits stay in their warrens during their diurnal resting phase. Domestic rabbits spend their short periods of resting overground. Likewise the circadian rhythm of feeding has undergone changes by domestication. Wild rabbits only feed at night and during the adjoining hours, with a maximum of feeding in the morning and another one in the evening. Domestic rabbits show no similar rhythm of feeding, and again remarkable individual differences are to be found.

The ascertained changes are possibly due to the absence of natural selection in domestication.

### Einleitung

Unsere Kenntnisse über tagesperiodische Prozesse beruhen zu einem großen Teil auf Untersuchungen, die an Haus- oder Labortieren vorgenommen wurden. HERRE und RÖHRS (1973) weisen jedoch darauf hin, daß circadiane und jahreszeitliche Rhythmen und deren Abhängigkeit von Zeitgebern bei Haustieren im Vergleich zur Wildform